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THE OCCURRENCE OF THREE RECOGNIZED COLOR MUTATIONS IN MICE

DR. C. C. LITTLE

HARVARD MEDICAL SCHOOL

THE common wild mouse, *Mus musculus*, has a type of coat-color pattern well known to geneticists as being characteristic of almost all wild species of rodents. This pattern is commonly called the ''agouti'' pattern. It consists in a ''ticking'' or ''banding'' of the hairs of both dorsal and ventral surfaces. On the dorsal surface each hair has a subapical band containing yellow pigment. The tip of the hair is black pigmented, while the half proximal to the yellow band is dark, containing both black and brown pigment granules. The general effect of the dorsal surface, when considered as a whole, is dull, brownish gray. The ventral surface is distinctly duller and paler than the dorsal. The distal half of the hair is lightly pigmented with black and occasionally with some yellow pigment, while the proximal half is much more heavily pigmented with black and brown granules. The general impression, conveyed by the ventral surface, is dull faded gray. This fact has led to the adoption by various investigators of the term ''gray-bellied agouti'' to describe the wild mouse color pattern.

In addition to this gray-bellied agouti another type of agouti house mouse has been reported as occurring wild in certain localities. This type has been used in genetic investigations by Cuénot and by Morgan.[1]

The chief difference between the gray-bellied agouti and the aberrant type is that the latter has, generally speaking, more yellow and brown and less black pigment. This is especially true of a band of hairs which runs laterally along the boundary of the lighter ventral hairs between the front and hind legs. This streak is very reddish in color and adds to the lighter and warmer coloring of the dorsal surface. Ventrally, the tips of the hairs are to all extents and purposes unpigmented and this produces a white or nearly white ventral surface. The proximal half of the hair is dark pigmented, a distinction between this type of white area and that found in spotted animals where the hair is white throughout its length. This type of agouti has been given the name of white-bellied agouti (gris à ventre blanc; Cuénot).

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[1] Morgan, noticing that Cuénot's mice of this variety had a small patch of reddish brown hair between the front legs while his own mice had not, has suggested the possibility that the variety with which he worked was not identical with that described by Cuénot. I have at present animals of this color variety with and without the spot and therefore hope soon to have a definite answer to this question.

In crosses with gray-bellied agouti the white-bellied form is epistatic. It can be obtained in a homozygous condition and is, as stated by Cuénot and by Morgan, one of a series of four allelomorphic forms of coat pigmentation.

It is the appearance of this epistatic "white-bellied" agouti in two experiments involving gray-bellied agouti and non-agouti mice that I wish to record.

EXPERIMENT *A*

In 1913, a cross was made between wild gray-bellied agouti mice and a race of dilute brown mice which I had started in the laboratory of the Bussey Institution.

The agouti race used was directly descended from wild animals without any out crossing with any domesticated mice. It therefore represented a stock of wild mice raised for several generations in captivity.

From this stock of agoutis I have recorded 531 young. All of them were gray-bellied agoutis[2] of the type that one might catch wild in any house. A certain amount of variation in intensity of pigmentation occurred among these mice. This variation, however, was not different so far as could be observed from that shown by a considerable number of specimens of this species from any single locality, judging from skins in the museum of comparative zoology of Harvard University. Among these skins, and among the mice raised from the gray-bellied agouti stock, there was not even an approach to the white-bellied agouti type.

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[2] The brown agoutis recorded later in this paper are of the dark or "gray-bellied" type.

The dilute brown animals which were used belonged to a race descended from a single pair of dilute brown mice which had been tested by suitable matings in order to establish their homozygosity. These animals in common with other "non-agouti" varieties of mice lack all visible traces of the agouti pattern and are with the exception of a slightly lighter ventral than dorsal surface uniformly pigmented throughout.

The cross between these two races, then, was one between a gray-bellied agouti and a "non-agouti" race. Both races used as parents were therefore color varieties which were hypostatic to the white-bellied agouti type and which for this reason could not carry that pattern as a recessive.

Four females of the dilute brown race were crossed with a gray-bellied agouti male 131 and produced 26 gray-bellied agouti young as shown in Table I.

TABLE I

GRAY-BELLIED AGOUTI

Mating	
♀ b1 × ♂ 131	6
♀ b2 × ♂ 131	8
♀ b3 × ♂ 131	6
♀ b4 × ♂ 131	6
	26

The F_1 gray-bellied agoutis were more intensely pigmented than their gray-bellied agouti parents. This deepening of color has frequently been observed in crossing wild agouti varieties with tame races and is probably due to modifying factors introduced by the particular tame race used or else to a general acceleration of pigment production due to heterozygosis.

The F_1 animals were crossed *inter se* and 285 F_2 young were raised. Of these 14 died at too early an age to have their color recorded.

In an earlier paper (1913), I have reported a cross similar to the one here recorded and have shown that three pairs of alternative mendelizing factors are involved. These are:

A—gray-bellied agouti.	a—non-agouti.
B—black pigment.	b—no black pigment.
D—intense pigmentation.	d—dilute pigmentation.

The gray-bellied agouti parent was homozygous for the factors for gray-bellied agouti, black and intensity being AABBDD in zygotic formula. The dilute brown parent was homozygous for the hypostatic conditions, non-agouti, no black pigment, and dilute pigmentation, and was, therefore, aabbdd in formula.

The F_1 gray-bellied agoutis would of course be heterozygous for all three pairs of factors and would be AaBbDd in formula. When such F_1 hybrids are crossed together, eight color classes of young are expected in a 27, 9, 9, 9, 3, 3, 3, 1 ratio. As will be seen from Table II, this result was approximated with the addition of a ninth and unexpected color variety, the white-bellied agouti.

TABLE II

	F_2 Generation									
Mating	Black Agouti Gray-belly	Black Agouti White-belly	Black	Brown Agouti	Dilute Black Agouti	Brown	Dilute Black	Dilute Brown Agouti	Dilute Brown	?
A 32×13	4	—	—	2	1	2	—	1	—	1
B 14×17	2	—	—	—	1	—	1	2	—	2
C 8×20	8	—	6	3	3	1	1	—	1	6
D 16×18	4	—	—	4	1	—	1	—	—	—
E 33×22	2	—	—	—	—	—	—	—	—	5
F 21×20	15	1	2	4	3	3	3	2	1	—
G 9×31	10	—	4	8	4	—	3	2	1	—
H 7×31	3	—	4	1	2	—	1	—	—	—
I 6×18	16	—	3	3	3	2	3	4	—	—
J 23×17	9	—	3	3	2	—	—	—	—	—
K 30×19	24	—	6	4	5	1	2	2	2	—
L 15×13	15	—	3	3	4	1	—	—	—	—
M 12×22	12	1	4	2	3	1	2	1	—	—
Obtained numbers	124	2	35	37	32	11	17	14	5	14
Expected on three factor basis	116.1	—	38.7	38.7	38.7	12.9	12.9	12.9	4.3	—

It will be noticed that the approximation to the expectancy on the basis of three pairs of Mendelian factors is extremely close. The occurrence of the two "white-bellied" agouti young is the matter of especial interest. These two young, one a male the other a female, are apparently identical with the gris à ventre blanc of Cuénot, judging from his description.

The question may quite naturally arise as to the possibility that the white-bellied agouti animals in F_2 had arisen by an accidental cross with some white-bellied agouti male in an adjoining cage. This possibility, however, is obviated by the fact that the F_2 generation white-bellied agoutis appeared in different cages at the Harvard Medical School where there had been *no other white-bellied agoutis* for more than a year before the appearance of the mutant animals. The two F_2 white-bellied agoutis must then be considered as true mutants epistatic to the type from which they originated.

Further evidence is provided by the F_3 generation, a tabulation of which is given below.

It will be observed that there is one "white-bellied" agouti among the 624 animals comprising the F_3 generation. This one mutant occurred as a descendant of a family of F_2 animals shown in Table II, mating J. This mating in F_2 gave 9 black agouti and 3 brown agouti young, none of which were "white-bellied" and the mutation therefore originated in a gamete formed by one of the F_2 generation animals while the other two white-bellied agoutis originated as mutations in the gametes of F_1 animals.

This recurrence of the mutation is a matter of considerable interest and indicates a germinal change, the occurrence of which is largely irregular, having some underlying cause or causes which become operative in animals of this particular hybrid race.

That hybridization between the same wild agouti and dilute brown races does not always produce this or any other recognizable mutation from the eight expected color

TABLE III

		F_3 Generation										
F_2 Parents	F_3 Mating	Black Agouti Gray-belly	Black Agouti White-belly	Black	Brown Agouti	Dilute Black Agouti	Brown	Dilute Black	Dilute Brown Agouti	Dilute Brown	Pink-eyed Black Agouti	Pink-eyed Dilute Black
M	164×161.....	2	—	—	2	—	—	—	—	—	—	—
	163×161.....	3	—	3	—	—	1	—	—	—	—	—
	72×76......	—	—	—	—	20	—	14	4	—	—	—
	163–164×161.....	14	—	1	11	—	2	—	—	—	—	—
L	331×335.....	—	—	—	2	—	—	—	—	—	—	—
	167×168.....	10	—	10	5	2	2	—	1	—	—	—
	165×168.....	2	—	1	—	—	—	1	—	—	—	—
	89×86......	12	—	—	—	6	—	—	—	—	—	—
	84×86......	16	—	—	—	9	—	—	—	—	—	—
	84–89×86......	30	—	—	—	3	—	—	—	—	—	—
	165–167×168.....	7	—	5	2	2	1	—	1	—	—	—
K	280×320.....	1	—	1	—	—	—	—	—	—	—	—
	130×135.....	3	—	2	2	—	2	—	—	—	—	—
	57×56......	3	—	2	7	1	—	—	1	2	—	—
	55×56......	2	—	6	—	—	—	1	—	—	—	—
	51×56......	4	—	6	2	—	2	—	—	—	—	—
	51–57×56......	3	—	4	1	2	1	1	2	1	—	—
J	145×142.....	4	—	—	2	—	1	1	3	1	—	—
	144×142.....	3	1	1	—	—	—	—	1	—	—	—
	91×93......	10	—	17	—	2	1	3	—	—	—	—
	90×93......	—	—	35	—	—	8	6	—	5	—	—
	144–145×142.....	3	—	1	—	3	—	—	1	—	—	—
F	136×137.....	9	—	1	3	—	—	—	—	—	—	—
	136–140×137.....	6	—	1	2	—	1	—	—	—	—	—
G	185×182.....	—	—	—	42	—	10	—	2	—	—	—
H	110×106.....	3	—	5	—	3	3	5	2	—	—	—
	102–103×101–105.	3	—	1	—	—	—	4	—	—	3	2
I	172–174×171.....	16	—	—	10	17	—	—	14	—	—	—
	80×78......	4	—	1	—	—	—	—	—	—	—	—
	79×78......	6	—	7	—	—	—	—	—	—	—	—
	79–80–82×78......	16	—	20	—	—	—	4	—	—	—	—
	79–80×78......	5	—	6	—	2	—	—	—	—	—	—
		200	1	137	93	72	35	40	32	9	3	2

varieties shown in Table II, is proved by the following experiments.

In 1911 a parallel cross was made between wild agouti and dilute brown races. The making of this cross I have recorded (1913; p. 55, Cross 20*a*; p. 52, Cross 10*a*, etc.) in a previous paper. The first hybrid generation consisted of gray-bellied black agouti animals, 8 in number. The second hybrid generation consisted of 55 animals which were of the expected color varieties. In the third hybrid and ensuing generations, including back crosses, I have recorded more than 4,500 young. None of these animals were white-bellied agoutis or indeed of any but the expected eight color varieties. This proves conclusively that the hybridization of these two races does not necessarily cause the white-bellied mutation to appear.

The fact that the white-bellied mutation has occurred in wild races of *Mus musculus* as shown by the capture of white-bellied mice would indicate that this mutation does not *necessarily* depend for its origin upon the presence in the germ cell of any of the recognized color factors *in a heterozygous condition.*

The test by breeding of the white-bellied agoutis obtained in the F_2 and F_3 generations has been attempted. One of F_2 generation mutants has not yet been bred, but the other F_2 and F_3 white-bellied agoutis have shown that their color pattern was epistatic to gray-bellied agouti and non-agouti. In these respects, the mutants have behaved in a manner identical with the gris à ventre blanc mice of Cuénot or the white-bellied agoutis of Morgan.

The observed facts therefore prove clearly the origin of this epistatic white-bellied agouti mutation at three different times in the course of this experiment.

It is interesting to note that there has been no selection in the direction in which the mutation occurred as was the case in the experiments of Castle and Phillips (1914) on hooded rats.

Although the white-bellied agouti may easily be considered merely an increased state of activity of the agouti factor beyond the gray-bellied stage, it is certain that it arises, not as the product of a series of small gradual changes, but suddenly and distinctly, without warning, and that after its appearance it behaves at once as a mendelizing character.

Taking into consideration the facts now recorded concerning this particular mutation we can say that its origin is apparently not solely dependent upon any of the known genetic processes. Inbreeding, hybridization, selection, none of them is indispensable to the occurrence of the mutation. The underlying cause or causes are at present clearly outside the bounds of analysis.

EXPERIMENT *B*

In 1912 I started, on a small scale, an experiment which had for its object the modification of the agouti pattern by repeated crossing with black (non-agouti) animals. It was thought that if the gametes of agouti animals showed quantitative variation in the factor underlying the agouti pattern repeated crossing with non-agoutis would succeed in decreasing the amount of the agouti character. It follows that if this was accomplished by contamination between the agouti gamete and the non-agouti (black) gamete, the non-agouti animals should show increasing traces of the agouti character as the agouti animals showed a diminution of that character.

The method followed was to cross black agouti animals derived from a sooty yellow stock with blacks from the same stock and selecting the blackest agoutis from each litter repeat the process. All the agoutis used were thus heterozygous for the agouti factor. This process was repeated for more than seven generations during which approximately 400 young were recorded. From the outset two facts were evident. *First, the agoutis grew distinctly blacker: second, there was no corresponding sign of contamination on the part of the non-agouti animals, but they too grew blacker.* It appears, therefore, that there was no sign of modification of the *factor* underlying the agouti pattern; but that a race was isolated by selection which showed a distinct increase in depth of pigmentation. In this connection it is interesting to note that while the agouti animals grew blacker and the yellow areas in the hair decreased *in extent,* the yellow pigment itself was a deeper richer yellow than that of the ordinary black agoutis. The yellow pigment had been increased in *depth* while the black pigment was being increased in *depth* and in *extent,* two entirely distinct processes.

All the agoutis up to the third generation were gray-bellied agoutis usually having more dark pigment on the ventral surface than is found in wild mice. In the third generation there occurred an agouti with a distinctly yellowish tinge to the under surface. The dorsal appearance of this animal was apparently the same as the other agoutis of this generation, a deep rich agouti with much black pigment. The ventral surface was, however, distinctly lighter in color than the other agoutis and showed a *decrease in dark pigment* as compared to them.

The yellow-bellied variation reappeared in the immediate progeny of the original yellow-bellied female and a race of these animals was established. When single mating tests were made to determine its behavior it *was found that when yellow-bellied agoutis one of whose parents was a non-agouti were crossed with non-agouti, only yellow-bellied agouti and non-agouti young resulted.* This fact indicated that yellow-bellied agouti fell somewhere in the series of multiple allelomorphs recorded by Cuénot and by Morgan.

At about this time English "black and tan" mice[3] crossed with white-bellied agoutis were found to give among their progeny agouti young almost identical with the yellow-bellied agoutis described above.

It at once suggested itself that the yellow-bellied agoutis occurring in my selection experiment were really *white-bellied agoutis* with one or more modifying factors which encouraged a higher degree of pigmentation than is normally found. This increase in an oxidation process would account for yellow pigment appearing in the tips of the ventral hairs which in ordinary white-bellied agoutis are unpigmented.

This supposition was further favored by the fact that as certain of the yellow-bellied agoutis grew to be old mice they showed a diminishing depth of pigmentation, *and developed typical white-bellied agouti coat color.* In old age they were not visibly different from some of the darkest white-bellied agoutis descended from a male of this variety kindly sent me by Professor Morgan.

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[3] Black and tan mice are a very dark type of yellow. Only a small amount of yellow appears on the sides, while the ventral surface is a deep rich reddish yellow. Black animals descended from black and tans are coal black with deep black ears, feet and tail.

One breeding experiment is interesting in showing the probable identical nature of the factor underlying the yellow-bellied and white-bellied agouti types. Two yellow-bellied agouti females known to carry non-agouti were mated with a white-bellied agouti male known also to carry non-agouti. On the supposition that the white-bellied and yellow-bellied mutations are the same, this mating should produce two types of young, agouti (either yellow or white-bellied, not both) and non-agouti in a 3:1 ratio. If on the other hand yellow-bellied agouti depended on a distinct factor falling in the multiple allelomorph series hypostatic to white-bellied agouti, the mating should produce three types of young, white-bellied agouti, yellow-bellied agouti, and non-agouti in a 2:1:1 ratio. Finally, if *yellow-bellied* agouti depended upon an *independent modifying factor which was acting upon a gray-bellied agouti animal,* one of two results should be obtained. If the factor was epistatic we should have white-bellied agoutis (plus the modifier), yellow-bellied agoutis and non-agoutis in a 2:1:1 ratio. If the modifier was hypostatic in the cross, white-bellied agouti, gray-bellied agouti and non-agouti young should occur in a 2:1:1 ratio. The three litters obtained have totaled 19 young; 11 white-bellied agouti and 8 non-agouti. The two classes of young seem to indicate strongly the correctness of the view that yellow-bellied agoutis are in reality white-bellied agoutis plus a darkening modifying factor or group of darkening modifiers the nature of which is not yet sufficiently clear to allow further description.

The point of extreme interest is that the white-bellied agouti mutation has occurred in a race which was being selected in directly the opposite direction from that taken by the variation. White-bellied agoutis represent a *stronger* agouti factor than the gray-bellied agouti factor, while every effort was being made in this experiment to weaken the gray-bellied agouti factor. It appears that the occurrence of the white-bellied mutation in experiment *A,* above recorded where *no selection* was being exercised, and the independent occurrence of the same mutation in experiment *B against* the course of selection are evidences that *the direction of mutation is largely if not entirely independent of selection and that the occurrence of the plus mutant rat in the plus selection series of Castle and Phillips before referred to, is in all probability a matter of coincidence rather than the result of selection as they have hinted.*

Pink-eyed Mutation

It will be noticed in the table showing the F_3 generation of the previous experiment (*A*) that among the 624 young recorded, 5 are pink-eyed. The pink-eyed mutation is hypostatic to dark-eye color and has been known for some time (see especially Castle and Little, 1909, Durham, 1911). These young all appeared in a single pen in which were two females and two males all of a single litter. Eight dark-eyed and five pink-eyed young were produced by these mice.

Up to the appearance of the pink-eyed young it was not suspected that the pink-eye factor in any way entered into the experiment. It was certain that one parent stock consisted of pure wild mice and that the pink-eye factor, which is a recessive, was not brought into the cross by this parent.

The pink-eye mutation, being recessive, could easily have been latent in the cross for some time without the combination of gametes necessary for its manifestation in a zygote having been realized. The dilute brown animals from which the second parent race was descended had originally been tested by breeding and had been found to be entirely free from the recessive pink-eye factor. Since, however, this mutation *appeared in only one F_3 family* it seemed distinctly unlikely that the original wild male, 131, which had been used as the male parent of all families, was the animal through whose gametes the mutation came into the cross. On the other hand, as there were four dilute brown females (Nos. b1, b2, b3, b4,) used in producing the F_1 generation, it seemed quite likely that one of these first introduced the pink-eye factor.

If such was the case the animal in question would be female No. b2. This mouse was the dilute brown ancestor of the particular group of F_2 animals which in turn were the parents of the pink-eyed mutant individuals.

The suggestion that the dilute brown parent is the animal which introduced the pink-eye factor is supported by the fact that *at about the same time at which the mutation appeared in the F_3 generation of this experiment it also appeared within the "pure" dilute brown race.* This makes it extremely probable that the mutation had already occurred within the dilute brown race and was brought into the cross by a single dilute brown female which because of the fact that it was dark-eyed concealed the presence of the recessive pink-eyed factor which in all probability existed in approximately half its gametes.

Unfortunately at the time that this mutation appeared in F_3 the dilute brown great grandparent had died. A breeding test was therefore impossible in order to ascertain whether she actually carried the pink-eye factor in one half of her gametes.

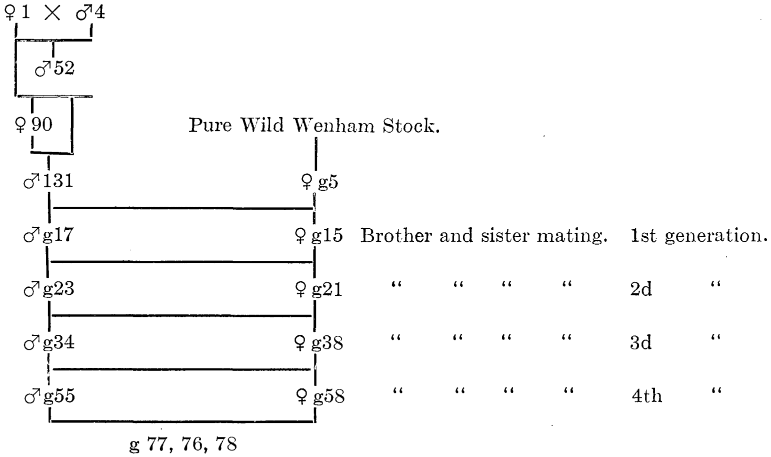
EXPERIMENT *C*

Another mutation, this time of the black producing factor, has occurred in a stock of pure wild mice, the original individuals of which were caught either in Wenham, Mass., or in Forest Hills, Mass., in 1912.

The particular family in which this mutation occurred is shown in Table IV. As will be seen, two wild mice both caught at Forest Hills, Mass., were bred together, these are female 1 and male 4. They and all their descendants, unless especial mention of the fact is made, will be considered black agouti in color. That is to say they were in appearance ordinary wild house mice. Female 1 and male 4 gave among their progeny male 52, who was crossed back to his mother and thus gave rise to female 90. She in turn was crossed back to her father, male 52, and from this mating male 131 was obtained.

TABLE IV

ANCESTRY OF BROWN-AGOUTI MUTANTS



8 Black agouti.
3 Brown Agouti.

Male 131 was used in many crosses, one of which was with female g5. This female was a pure wild mouse taken from a stock pen of wild mice which for several generations had been reared in captivity by Dr. J. C. Phillips at Wenham, Mass. From this mating came 6 black agouti young in a single litter. Two of these young, female g15 and male g17, brother and sister, were mated together and produced 11 black agouti young, two of which, male g23 and female g21, were mated together. This brother and sister mating gave 16 black agouti young from which another brother and sister mating, male g34 and female g38, was made. From this pair was obtained 13 black agouti young, among which were male g55 and female g58, the parents of the mutants. These two mice male g55 and female g58 have had three litters of young. The first born in December, 1915, consisted of three animals, male g77 *Brown Agouti,* female g78 *Brown Agouti* and female g76 *Black Agouti.* The appearance of the brown agoutis was entirely unexpected and was thought to be possibly due to an error in records. A second litter however, born in February 1916 after the parents had been under careful observation, consisted of two black agoutis, a male and a female, and *one brown agouti a female*. The third litter of five is all black agouti.

This is a clear case of mutation within a closely inbred race, and is interesting to contrast with Experiment *A* already referred to, in which a mutation occurred in hybrids.

There is one fact of possible interest in connection with the mutations recorded in Experiment *A* and in this experiment. Male 131, black agouti, is a common ancestor of all the races in which the mutations occurred. It has been shown that the evidence is *against* his having introduced the pink-eyed mutation and that this probably came from the dilute brown race.

For the other two mutations, however, the white-bellied agouti and the brown agouti types, it is theoretically possible that male 131 possessed or transmitted an instability of germplasm which has manifested itself in the cropping out of these mutations among his descendants. Fortunately the stock within which the brown agouti mutation arose is being carried on in single pair, brother and sister, matings. By this method we should be able to recognize mutations at the earliest possible moment after their occurrence.

Summary

To sum up the facts above recorded it may be stated that:

1. A previously recorded mutation of the gray-bellied agouti pattern, known as white-bellied agouti, has arisen in two experiments on color inheritance in mice.
2. In experiment *A* it has arisen independently three times in a hybrid race of mice.
3. In this experiment there has been no selection in the direction of the mutation.
4. In experiment *B* it has arisen once in an inbred race in which selection was being carried on.
5. In this race the mutation represents a variation in

exactly the opposite direction from that in which the selection was being made.

6. A recessive pink-eyed mutation has occurred in a closely inbred dilute brown race. A similar mutation has appeared in a hybrid race into which one animal from the dilute brown race probably introduced the mutation.

7. A mutation involving loss or suppression of the black producing factor has arisen in a stock of inbred wild mice. This has caused the appearance of brown agouti young.

8. The wild race in which this occurred is related to the hybrid race (see conclusion 2) in which the white-bellied agouti mutation appeared three times. The suggestion is offered that a tendency to germinal instability may have been transmitted by male 131 a common ancestor of both races.

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